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SOME ASPECTS OF ISLAND ECOSYSTEMS ANALYSIS

(A preliminary conceptual synthesis)

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ISLAND ECOSYSTEMS IRP

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ABSTRACT

The point is made that ecological principles generated from the study of continental ecosystems cannot be extrapolated to oceanic islands without reservations. Island ecosystems are not necessarily unique at the level of biome or formation structure, but they differ greatly at the level of life form and species structure, and as such, they differ also in their functional and dynamic relations. The greatest departure occurs in the area of species interaction. Examples of such departures are given in three areas of ecosystem analysis:

(1) Spatial distribution of island biota,

(2) Niche differentiation, and

(3) Successional phenomena.

The differences in ecological relationships of oceanic island ecosystems are a direct reflection of their special biological evolution, caused by geographic isolation, small habitat size and recent geological age. Perhaps more so than elsewhere, ecosystem analysis on islands cannot be meaningful without an appreciation of their special evolutionary relationships. However, to some extent this applies also when trying to extrapolate results of ecosystem analysis from one biogeographic region to another. It is suggested that the ecological consequences of different biological evolutions are best recognized by studying ecologically similar species within the context of their general niches and by relating these to the ecosystem as a whole.

SOME ASPECTS OF ISLAND ECOSYSTEMS ANALYSIS

Dieter Mueller-Dombois

Perhaps you may concur with my assumption that the reason for emphasizing the subject matter of TROPICAL ECOLOGY is a general realization that ecological principles developed through the study of TEMPERATE ECOLOGY are not always sufficiently complete to explain important ecological relations in the tropics.

My thesis in this presentation is that ISLAND ECOLOGY differs enough from CONTINENTAL ECOLOGY that ecological principles developed from the study of continental ecosystems are not always sufficiently complete to explain important ecological relations on islands.

The peculiarities of island life have received considerable attention by evolutionary biologists since Darwin (1859) developed his theory of speciation from his observations of the Galápagos finches. Carlquist (1965, 1970) presented comprehensive reviews together with theories that may explain the often rather bizarre life forms developed on isolated islands. Fosberg (1963, 1966, 1967) and others (e.g., Dorst 1972) have written conceptual papers dealing with the precarious balance and fragility of island ecosystems.

It is not my intention to review the findings of evolutionary biology, but rather to point out how biological evolution enters into the study of ecosystems analysis on islands as carried out currently by the Island Ecosystems Integrated Research Program of the U.S. International Biological Program (IBP).

THREE IMPORTANT FACTORS

The first and most important factor is the GEOGRAPHIC ISOLATION of

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island ecosystems. In this respect the Hawaiian Islands are perhaps one of the best case examples. The Islands are 2,000 miles away from the nearest continent to the east, North America. (The distance to the Philippines is 5,300 miles, to Japan 2,500 miles, to Australia 4,000 miles. The nearest Island is Johnston Island, 450 miles SW, the Line Islands, 1,000 miles S, and Wake Island 1,200 miles SW.)

The second factor is SIZE. Different opinions exist with regard to defining Australia as an island or continent, but, as a rule, islands are small land masses.

A third factor is AGE. There are islands, so-called continental islands like Ceylon, that are as old geologically as the continental land mass from which they originated. However, oceanic islands are of volcanic origin. If they are still mountainous, they are as a rule, geologically of relatively recent origin. The age of the oldest parts of the high Hawaiian Islands is estimated as 11.3 million years (Macdonald and Abbott 1970).

These three factors have important bioecological consequences.

Geographic isolation is responsible for a "screening effect" on the number of kinds of biota that can get there. Only those amenable to long-distance transfer could become established before the arrival of man. The present native flora of Hawaii has been estimated by Fosberg (1948) to consist of a little over 1,700 species and varieties. However, through the study of taxonomic relationships, he estimated this flora to have formed from only 272 original arrival forms that became successfully established. A few of these have not changed morphologically; the indigenous species. Others have changed morpho-genetically by having formed populations that deviate taxonomically from their nearest relatives elsewhere, or that became fractured into many distinct species and varieties; the endemic taxa. Endemism in the vascular

flora is estimated to be in excess of 95% meaning that over 1,600 of the native Hawaiian species and varieties do not occur anywhere else in the world.

While geographic isolation is responsible for the unique biota of Hawaii, it is not simply distance over water and disseminule size that has determined the composition of the native flora. If this were so, the Hawaiian flora should show the greatest similarity to the North American temperate and sub-tropical flora. Instead, 71% of its flora is of tropical, 19% of temperate and 10% of unknown origin. The high tropical component is most likely a reflection of a habitat selection for successful establishment of plants pre-adapted to tropical climates. The 19% temperate plant forms may have found suitable habitat conditions at higher elevations. However, one should remember that the cool climates in tropical mountains differ greatly from the climates in the temperate zone. Temperate life forms, to be successful in tropical mountains, must tolerate a near-absence of seasonal temperate and day-length changes.

(Of the 71% native vascular Hawaiian plant taxa of tropical origin, 40.1% show Indo-Malayan, 18.3% tropical American and 12.5% pan-tropical affinities. Of the 19% plant taxa of temperate origin, 16% show Australian and only 3% north temperate origin. Thus the major successful invasion came from the southwest in spite of the greater distance to major land masses in that direction.)

The biological implication of "small land size" associated generally with islands is that population sizes of perennial organisms are also small. Even in the mountainous islands, which usually have much greater land masses than flat coral islands, the recurrence of similar habitats is rather limited in comparison to most continental mountain ecosystems. Small areas for populations to develop on implies limitations in gene-flow as well as number of individuals. Both factors contribute to a greater fragility of island

populations.

The bioecological consequence of the third condition, "recent geological age," is that, for example, tropical island rain forests are much younger than most tropical continental forests. The latter may have undergone more or less uninterrupted succession from giant equisetum-lycopod and seed fern forests to primitive gymnosperm and angiosperm forests, and then to the modern angiosperm forests. In contrast, the origin of most existing volcanic island forests is within the modern angiosperm era. As mentioned before, the oldest parts of the high Hawaiian Islands are estimated as being only 11 million years old. Fosberg (1948) estimated that only one arrival form was required to become successfully established every 20,000 - 30,000 years to account for today's native flora of > 1,700 taxa. The shorter geological time available for community development may in part account for a lower alpha diversity in tropical island communities as compared to tropical mainland communities.

It may be argued that the three conditions mentioned; isolation, small size, and recent geological age are not entirely unique to islands. However, the biological consequences of these conditions are most clearly developed on islands.

The main point is that these conditions have caused a different evolution in island ecosystems. Thus, on islands, more so perhaps than in biogeographically different continental ecosystems, the effect of a unique evolution becomes evident in many ecological relationships. The ecological relationships primarily involve the interactions among native species, and among native and exotic species. Many of the latter were introduced by man within the last 200 years. He thus affectively broke the natural isolation barrier.

I will now try to explain some peculiarities of island ecology as they are beginning to emerge in three areas of ecosystem analysis that are being

investigated in the ISLAND ECOSYSTEMS Integrated Research Program of the US/IBP. The three areas are (1) spatial distribution of island biota, (2) community structure and niche differentiation, and (3) successional phenomena.

The ecological relationships in these three areas have to do mostly with species interactions in an ecosystem context, rather than with metabolic process research of ecosystems as pursued in the US/IBP Biome Studies. Because of the unique evolution of the island biota, we are concerned primarily with the interaction of native and exotic species.

SPATIAL DISTRIBUTION OF ISLAND BIOTA

Ecological amplitudes

In contrast to most tropical continental vegetations, the native forest vegetation of the Hawaiian Islands is remarkably simple. There are, in fact, only two dominant, tall-growing (25-30 m maximum) native tree species, Metrosideros collina (with several varieties) and Acacia koa (with few varieties). These are wide ranging dominants whose spatial distribution can be ecologically characterized as follows (FIG. 1):

On the most southern Island Hawaii (the so-called "Big Island" with an area of 4,038 square miles), Metrosideros ranges from sea level to 8,200 feet (2,500 m) elevation on Mauna Loa (13,677 feet = 4,170 m). In terms of climatic parameters this means that the tree grows in a year-round warm-tropical climate of 23°C mean air temperature all the way up into a cool-tropical, high-altitude climate of 8°C mean air temperature. The upper boundary of Metrosideros is marked approximately by the year-round nocturnal ground-frost boundary (Mueller-Dombois 1967). Acacia koa has a more limited range on Mauna Loa from 4,000-6,700 feet (1,220-2,043 m), within the range of Metrosideros. On Mauna Kea (13,796 feet = 4,206 m) and on the island of Maui, Acacia koa occurs in a similar high altitude range as on Mauna Loa, but it also occurs in the

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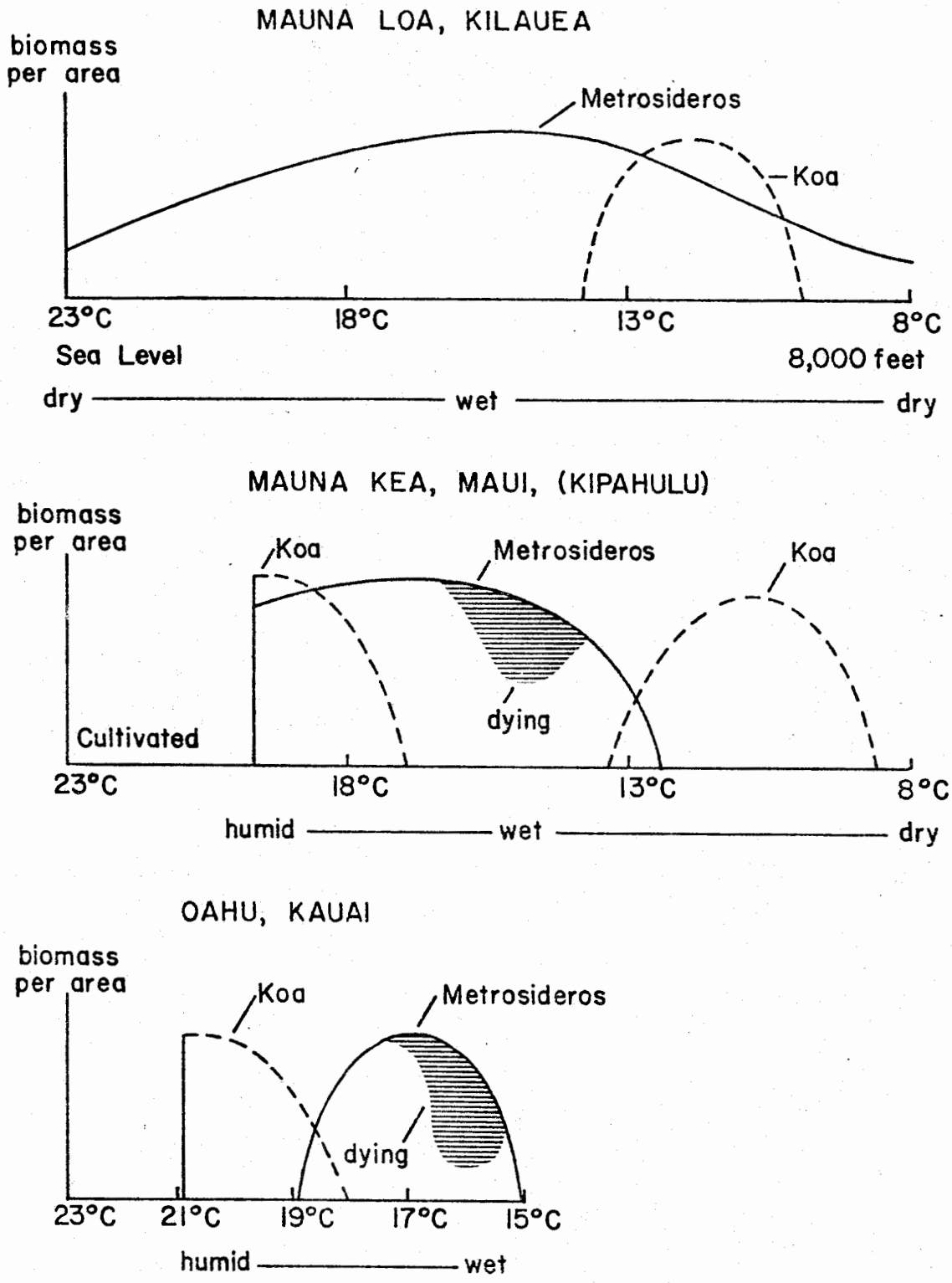

FIG. 1. General ecological amplitudes of the two most important native tree species (Metrosideros collina and Acacia koa) in the mountainous Hawaiian Islands.

lower montane belt together with Metrosideros. On the islands of Oahu and Kauai, Acacia koa only occurs below the range of Metrosideros, and the two species rarely form mixed stands. However, a few widely scattered or rare Metrosideros individuals of shrub-stature do occur down to 500 feet (150 m) on Oahu and to sea level on Kauai.

The change in range of these species is correlated with substrate age. Mauna Loa is still an active volcano whose currently exposed lava rock substrate ages range from probably post-pleistocene to present. In contrast, most of the Mauna Kea surfaces are from late pleistocene (from 600,000 to about 15,000 years ago). The substrates on Oahu and Kauai are from 1-6 million years old (Macdonald and Abbott 1970). The substrate age effect is primarily one of changing soil water regimes, from xeric to hydromorphic, in the mid-elevation rain forest range. The dying Metrosideros in the wet areas on the older substrates is often correlated with poor drainage. However, correlation with substrate age and soil moisture regime does not mean that those factors are also the causes of these distributions. The causes are as yet unknown.

Several other native woody life forms of small-tree or shrub stature have similarly wide-ranging (but often interrupted) distributions, for example, the trees Myoporum sandwicense, Sophora chrysophylla and the shrub Styphelia tameiameia (which may be split into low (S. tameiameia) and high elevation (S. douglasii) species). Other species of similar life form have peculiarly narrow ranges. Such species may belong, however, to wide ranging genera, such as the shrub Cyrtandra, which apparently occurs with 118 species on Oahu (St. John 1966), an indication that this group has been fractioned by adaptive radiation. These fractioned taxa are responsible for another ecological peculiarity, found mostly on the older volcanic islands, namely that physically

similar habitats may be occupied by quite dissimilar communities in terms of species composition. Thus, the pattern of recurrence of similar species combinations in similar habitats varies between islands and generally decreases with island age.

Hypotheses of species distribution

Based on a working hypothesis: that endemic birds, insects and other subsidiary life forms evolved primarily in adaptation to the community-structure forming dominant native plant species, we are testing the degree of spatial association of native biota along environmental gradients. Our current test gradient is a 22 mile-long transect on the east flank of Mauna Loa, which cuts through 12 structurally well-defined vegetation types, i.e. from alpine scrub to Metrosideros-Cibotium (tree fern) rain forest, from 10,000 feet (3,049 m) to 4,000 feet (1,220 m) elevations. Both tree species, Metrosideros collina and Acacia koa, form the structural dominants in these ecosystems, and we are trying to find out specifically whether native ecosystem stability is here related to the biomass (as defined by density and height) of these two major native tree species. As an initial index of native ecosystem stability we will use the proportion of native and exotic population sizes within life form groups of an ecosystem, realizing, however, that stability involves persistence over time in the presence of certain disrupting forces or perturbations.

So far, this hypothesis appears to be supported by the distribution study of phytophagous insects (Gagne 1972), but not, for example, by the soil arthropods (Radovsky 1972). In the former group many endemic species are found where these two tree species are most vigorous, while among the soil arthropods most species are exotics. The latter show wide distributions, quite

unrelated to the vigor or distributional variations of the native tree species and ecosystems.

There are currently four hypotheses about species and community distribution along environmental gradients. These have recently been stated by Whittaker in his 1970 textbook (Whittaker 1970: 35) as follows:

1. "Competing [dominant] species exclude one another along sharp boundaries. Other species evolve toward close association with the dominants and toward adaptation for living with one another." (This species distribution would result in distinct zones.)
2. "Competing [dominant] species exclude one another along sharp boundaries, but [other species] do not become organized into groups with parallel distributions." (This would result in zones with overlapping species ranges.)
3. "Competition does not [usually] result in sharp boundaries [i.e. zonation] between species populations. Evolution of species toward adaptation to one another will, however, result in the appearance of groups of species with similar distribution." (This would result in a pattern of typical communities separated by ecotones.)
4. "Competition does not usually result in sharp boundaries between species populations, and evolution to one another does not result in the formation of groups with similar distributions. Instead, centers and boundaries of species populations are scattered along environmental gradients." (This would result in no recognizable zonation and absence of typical communities.)

All of the four spatial distribution patterns seem to be possible. Whittaker's studies in continental temperate mountain ecosystems supported the last named hypothesis. Our studies in island tropical mountain ecosystems seem to support the third hypothesis as far as the native biota are concerned.

Moreover, Whittaker (1970) holds that the highest degree of integration is accomplished by a high beta-diversity. High beta-diversity implies accomodation of a large number of species with restricted distributions along a given environmental gradient as opposed to a few wide-ranging species on the same gradient. Low beta-diversity appears to be a characteristic along altitudinal gradients on oceanic islands, at least in Hawaii. In the tropics, this is a peculiarity. Whether this also means poor integration, needs further examination. An increase of beta-diversity through exotic species invasion appears to show the opposite, namely a decrease in integration.

COMMUNITY STRUCTURE AND NICHE DIFFERENTIATION

For the purpose of distinguishing ecological peculiarities in island communities and ecosystems, we may recognize three levels of community structure.

1) Gross structure at the level of formation or biome
2) Fine structure at the level of the species assemblage
3) Intermediate structure at the level of species groups with similar gross-morphologies (life forms) and/or similar general ecological adaptations.

Biome structure

On the basis of gross structure, island communities and ecosystems are not unique. For example, on the island of Hawaii alone, we have nearly all types of formations represented. We have alpine tundra, open and closed scrub, evergreen rain forest, evergreen seasonal forest, savanna, grassland, desert, and other formations. Moreover, several of these formations show quite similar general habitat relations as in continental tropical lowland and mountain ecosystems. In addition to gross-structural similarities, one can recognize even certain gross-taxonomical relationships among equivalent island and continental formations. To give a general altitudinal outline: The leeward lowlands have a

winter rainfall and a summer-drought climate. Most typical is the perennial grass savanna. The woody plants may be scattered trees or shrubs, or shrubs variously clumped. Among trees, members of the Leguminosae are important. Open seasonal evergreen forest occurs above this lowland vegetation on the leeward side. Where well-preserved, this is a taxonomically quite rich tree vegetation, with at least 20 native tree species (Wirawan 1972). In the montane environment, evergreen rain forest predominates with Myrtaceae (Metrosideros, Eugenia, also with introduced taxa, Psidium spp.) and native tree ferns (Cibotium spp.). Above the rain forest occurs mountain parkland or savanna. There, legume trees are again important (Acacia, Sophora). Above this, subalpine open forest and scrub occurs. The scrub shows "heath," i.e., shrubby members of Ericaceae (Vaccinium spp) and those of a closely related family, Epacridaceae (Styphelia). In the alpine scrub and near the tree line one may find (today much diminished) individuals of the peculiar tree-like hapaxanthus plants. In Hawaii, these are the silverswords (Argyroxiphium spp.). The homologs in the tropical Andes are the giant espeletias, on Kilimanjaro, the tree-like senecios. These three taxa are from the same family, Compositae. Above these, and the sparse alpine scrub, is an alpine tundra or stone desert with a sparse moss (Rhacomitrium lanuginosum) and/or crustose lichen (e.g., Lecanora spp.) growth. This general sequence of altitudinal formations is quite similar to several continental tropical mountains (Troll in Walter 1971). Thus, on the level of gross structure, island ecosystems are not at all unique. The same applies probably also to gross functions such as photosynthesis and productivity, decomposition, mineral cycling, i.e., to the general ecosystem metabolism, which is not expected to show great differences between tropical island and continental formations.

Niche differentiation

At the level of fine-structure, however, island communities and ecosystems

are totally unique because not only do we find different species assemblages in habitats otherwise roughly similar to continental ones, but we may also encounter quite different spatial relations along environmental gradients. For this reason, specific functions are also expected to be unique.

We may best recognize the degree of departure of island ecosystems in comparison with continental ecosystems at the level of intermediate structure. Above, I have defined this level as consisting of "species groups with similar gross-morphologies (life forms) and/or similar general ecological adaptations." In plant ecology, we have the term "synusia" (Gams 1918, Lippma 1939) for species of similar life forms occurring together in the same habitat. In animal ecology, there exists to my knowledge, no directly equivalent concept. However, on a functional level there is the term general niche (Miller 1967).

The concept of niche can be defined as "the space occupied by an organism and the functional role that it assumes in that space." It is useful to distinguish between "specific" and "general" niche. A specific niche is the space and function in that space as demonstrated by a species population within an ecosystem. In contrast, a general niche is the space and function in that space as demonstrated by a group of species of closely similar ecological adaptation. A functional plant ecological concept for the species occupying a general niche is that of "ecological group" (Ellenberg 1956), which could also be applied to animals and microorganisms that have a general niche in common.

In the ISLAND ECOSYSTEMS Research Program of the US/IBP, we found it useful to integrate our studies on the basis of ecological groups and the general niches that these groups occupy. This, we believe will form the best basis for biogeographic and ecological comparisons of the structure and function of ecosystems.

We are currently studying the following ecological groups in two areas; a) along an altitudinal ecosystem gradient and b) in a 200 acre plot of a large

homogeneous montane rain forest:

(1) phytophagous insects (sap-sucking insects, leaf miners, etc.)

(2) bark and wood beetles

(3) seed feeders

(4) fruit flies

(5) litter insects

(6) soil arthropods

(7) soil fungi

(8) soil algae

(9) litter fungi

(10) phyllosphere fungi

(11) forest birds (pollinators, seed feeders and dispersers)

(12) introduced (only) rodents (predators, small herbivores and seed feeders & dispersers)

On a similar basis we are studying the plant synusiae in the rain forest community:

(13) the canopy and emergent trees

(14) the subordinate trees

(15) the shrubs

(16) the woody plant seedlings

(17) the herbaceous ground-rooting plants

(18) the vascular epiphytes

(19) the mosses and liverworts on the forest floor

This approach allows to recognize ecosystem peculiarities and to study ecosystem integration from a variety of viewpoints. First of all, we can recognize many gaps. Several of these are caused by funding limitations and lack of specialists and integrators. For example, we have not yet covered the

epiphytic bryophyte and filmy fern synusia or the lichen synusia among primary producers. We have not covered insect pollinators and pollination biology in general. The latter is an integrative function. Seed and fruit consumption and dispersal will be integrated from bird and rodent behavior studies, but there may be still other forms of disseminule distribution, for example, that by introduced feral pigs. Other gaps are real in the sense that a general niche may be totally unoccupied. This applies to the large-herbivore niche, which did not become established naturally in the Hawaiian Islands. However, introduced herbivores, such as goats and pigs, do occupy a rather destructive role as will be referred to later. The disseminule dispersal niche appears to be poorly represented in Hawaii. Only one native mammal (Tomich 1969), the hoary bat (Lasiurus cinereus semotus H. Allen) may have contributed to this niche-function. Forest birds seem to occupy very restricted territories. Absence of effective native fruit dispersal agents in Hawaiian ecosystems may explain in part the presence of many rare or small species populations in different localized parts of the Hawaiian rain forest.

The often talked about relationship of diversity and stability makes a great deal more sense when studied in the context of general niches rather than specific niches. For example, a brief analysis of primary producer niches in the montane tropical island rain forest shows the following:

(1) Upper tree canopy synusia: only 2 species, one decidedly dominant in crown cover (Acacia koa)

(2) Subordinate tree synusia: 10 species, 1 decidedly abundant (Metrosideros collina), 4 scattered species (Cheirodendron trigynum, Ilex anomala, Pelea clusiaefolia, P. sandwichiana), the rest are rare species (Myrsine lessertiana, M. sandwicensis, Coprosma rhynchocarpa, Broussaisia sp., Myoporum sandwicense).

(3) Shrub synusia: greatest foliar biomass, because of high density of tree ferns (Cibotium spp.). In addition several native shrubs (Rubus hawaiiensis, Pipturus hawaiiensis, Vaccinium calycinum, Cyrtandra lysiosepala, among others).

(4) Woody plant seedlings: numerous small seedlings of Metrosideros on fallen and decaying logs. Mineral soil rarely occupied by seedlings. Cheirodendron seedlings common (also on logs).

(5) Vascular epiphyte synusia: widely scattered individuals of Astelia menziesiana (Liliaceae), several scattered ferns (Elaphaglossum hirtum, Polypodium pellucidum, Pleopeltis thunbergiana). Mostly on branches of Acacia koa.

(6) Herbaceous ground-rooting plants: very little biomass because they are widely scattered. Native plants of only fern species (Dryopteris paleacea, Asplenium contiguum, A. lobulatum, Pteris excelsa, Cyclosoris sandwichensis, among others), several introduced forbs, mostly composite weeds (Eupatorium riparium, Erechtites valerianaefolia, Senecio sylvaticus, Hypochaeris radicata).

(7) The moss and liverwort synusia: about 20 species (abundant, Rhizogonium spiniforme, Campylopus sp., Lencobryum gracile, Hypnum sp.). All restricted to decaying wood on ground.

In addition to the low diversity of the canopy tree synusia, another island peculiarity appears to be the absence of native forbs in the herbaceous ground-rooted synusia. Here, only ferns have become established, and only in low quantities. It is in this synusia that exotic plants invaded into this otherwise completely native community. The reason, however, is not merely poor occupation of this general niche by native herbaceous species, but more particularly the influence of pigs which disturb the forest floor abundantly. Pigs were first

introduced by the Hawaiians 1,000-2,000 years ago. Europeans introduced more pigs within the last 200 years. Nevertheless, the number of native species of plants and their quantitative occupation of the general niches may provide a useful index to predict stability, i.e., here meaning resistence offered against invasion of exotic biota of similar ecological adaptation. A general plant niche practically unfilled is the vine or liana synusia. In this forest there is only a very thin-stemmed (probably rather slow-growing) woody vine, Alyxia olivaeformis. The native Rubus hawaiiensis shrub sometimes grows as a vine, but with upward growth limited at a 5-8 m height. An introduced vine from tropical South America, Passiflora mixta has recently spread vigorously in another similar forest (about 40 miles away on Mauna Kea). This vine has assumed epidemic proportions by forming dense curtains from the ground to the canopy of the tallest (25-30 m) Acacia koa trees, killing many members of the subordinate tree and shrub synusia. This exotic vine is so successful because it is filling a practically empty niche. But here the original structure of the ecosystem was also destroyed in part during several decades of cattle grazing. Cattle and pig activity had practically eliminated the woody seedling and shrub synusiae, including the tree ferns, thereby aiding in the establishment and spread of this exotic vine.

SUCCESSIONAL PHENOMENA

Succession relates to a change in the biotic community on the same site that is directional rather than rhythmic, a change that once started from a perturbation of some sort, continues for a period of at least several years before the rate of change becomes non-measurable.

In island community succession, it is particularly the interaction of man-introduced (exotic) and native species that can bring about some important

ecological consequences. Recently, we completed several studies on succession or their effects. Some of the results can be summarized under two subheadings:

(a) Replacement by exotic species

(b) Recovery trends of native species

Replacement by exotic species

A closed perennial grassland occurs in the mountain parkland ecosystem on the east flank of Mauna Loa (4,500-6,700 feet/elevation or 1,370-2,040 m). It has a simple composition of about 10 herbaceous species. The currently most dominant grasses are the native Deschampsia australis and the European Holcus lanatus. The latter was first collected in 1903 (Whitney et al. 1939). During a detailed reconnaissance in 1965, I noticed that Holcus lanatus appeared to be more common on areas that were scarified or dug-up by feral pigs (Mueller-Dombois 1967). From 1971-72 we did a detailed experimental study to determine whether pig-digging aided in the spread of the introduced grass (Spatz and Mueller-Dombois 1972b). We found that both grasses participated in the invasion of freshly scarified soil, but that the rate of invasion of Holcus exceeded that of Deschampsia considerably. For example, a place that contained about 60% Deschampsia and only 25% Holcus before ground disturbance, had after one year a plant cover of 30%, of which about 15% was Holcus and less than 5% was Deschampsia. Areas with no noticeable ground disturbance are still dominated by the native grass. Thus, it seems clear from this study that the invasion of the exotic Holcus lanatus is decidedly favored by pig-digging.

The general replacement of a formerly native grassland by an exotic grassland has perhaps no serious ecological consequences, unless a number of other native biota are also threatened. However, since the area is in a National Park where the policy is to preserve the native ecosystems in their natural state, an important value judgment is involved. This relates to the elimination of

feral pigs from the Park area, because the pigs represent a new stress factor that did not exist during island ecosystem evolution.

Another example of grassland establishment seems to have more serious ecological consequences. An Eastern North American grass, Andropogon virginicus (broomsedge), was noticed on Oahu, Hawaii in 1932 (Rotar 1968). This grass spread, and today it forms the dominant herbaceous cover in all denuded lowland (up to about 800 feet or 250 m elevation) rain forest habitats on windward Oahu. The grass is clearly a fire-adapted bunchgrass that accumulates dead standing yellow foliage in a few years. In addition, it goes into dormancy during the winter months just when the rainfall increases on windward Oahu. At that time of the year, in particular, the broomsedge grass cover forms a straw-like mulch that reduces evapotranspiration from the surface, and this is in an area where excess water is a problem. Transpiration rate studies have shown that the Andropogon grass cover removes only a fraction (about 20-25%) of the incoming rain water during the winter months, October through April (Mueller-Dombois 1972a). On the same habitat, evergreen trees remove considerably more water because they maintain a much greater quantity of active leaf material on a square meter basis (2.24 kg/m^2 green foliage for the trees versus 0.58 kg/m^2 green blades for the grass). The habitat shows considerable erosion and runoff, much of which can indirectly be attributed to the introduced grass.

The dominance of Andropogon is maintained by periodic accidental fires. Apparently no other grass is available locally that can compete with Andropogon. In a similar continental tropical ecosystem, the winter-dormant Andropogon would probably not have become established. Here, instead, a fire-adapted grass would have taken its place; one that would remain green during the season of higher rainfall. This applies, for example, to Cymbopogon nardus in the continental island of Ceylon.

Recovery trends of native species

Succession on new volcanic surfaces. - Plant invasion and recovery after a volcanic eruption was studied for nine years in a rain forest location (Smathers and Mueller-Dombois 1972) on a number of new volcanic habitats at the Kilauea Crater in Hawaii. Among other things, the rate and sequence of plant life form invasion was recorded. On a pahoehoe lava rock habitat, algae, mosses and ferns arrived in the first year after new surface deposition. Lichens arrived in the third year and seed plants in the fourth year. The seed plants, consisted of five species, four of these were native woody plants (Metrosideros collina seedlings, Vaccinium reticulatum, Dubautia scabra and Hedyotis centhranthoides), one was an exotic species (Lythrum maritimum). As time went on, the frequency of the four native seed plants increased more uniformly over the new surface, but they were always found in the rock crevisses. The exotic species disappeared, but other exotics became established, grasses in particular (Paspalum conjugatum, P. dilatatum, Andropogon virginicus and Setaria geniculata). These remained only in a very restricted area in a moister microhabitat.

Next to an undisturbed rain forest, several exotic woody plants (Buddleja asiatica, Rubus rosaefolius and Rubus penetrans) advanced quickly onto an ash surface. The exotics became established mostly at the base of standing snags, where the moisture relations were more favorable. However, native woody seed plants also became established. After a few years, considerable mortality was observed among the exotic woody plants (Buddleja, in particular), but not among the native species. Moreover, some individuals of the exotic Rubus shrubs were encroached and then replaced by native shrubs (Dubautia scabra and Vaccinium reticulatum) indicating competitive replacement. Here exotic grass species also arrived, but they remained so far confined to moister microhabitats.

The results show that, in general, native pioneer species are better adapted

to the new, edaphically extreme habitats. However, exotic species participate in primary succession. Particularly those exotics appear to be successful that receive no or little competition from native plants. For example, no pioneer grasses have evolved in the Hawaiian rain forest. Exotic grasses, therefore, fill a vacant niche in primary succession on lava and ash surfaces in rain forest climates.

Recovery following experimental herbivore displacement. - As pointed out before, the mammalian herbivore niche was not filled in the course of island evolution. However, several large herbivores were introduced to the islands by the Europeans. Among these, goats became particularly abundant on the Island of Hawaii, where they were introduced about 200 years ago.

Goat concentration centers occur in the seasonally dry climates in the mountain parkland ecosystem and the coastal lowland of Hawaii Volcanoes National Park. Following a mapping project of the Park's vegetation, I suggested establishment of several goat exclosures in these two areas.

A 10 m by 100 m goat exclosure was built in the mountain parkland in 1968. The exclosure was established in the grassland adjacaent to an Acacia koa (koa) stand. Koa reproduces in the mountain parkland from root suckers, while in the rain forest, it reproduces primarily from seed.

In 1971, a quantitative analysis was made (Spatz and Mueller-Dombois 1972a). At that time, the exclosure was stocked with a dense sapling stand of koa suckers from 10 cm to 2 m tall, while hardly any suckers of this size occurred outside the exclosure. However, a very large number ($> 3/m^2$) of small (< 5 cm) herbaceous root suckers were found outside. A structural survey of koa was made throughout the mountain parkland, and the general trend was similar to the outside-exclosure pattern; i.e., a large number of small herbaceous suckers, very few taller woody saplings. Among the few taller woody saplings, about 50% were girdled

and defoliated, had broken stems, or were dead and still standing.

This result shows two things that may be of evolutionary significance:

(1) That koa has a tremendous capacity to resprout, when its small herbaceous suckers are browsed,

(2) That koa has no capacity to resprout when the woody saplings are girdled or broken from browsing.

The capacity to resprout from roots appears to be an adaptation to grow competitively within closed grassland. Sprouting may also be encouraged by grass burning or ash fall-out from volcanic explosions. Fire appears to be a natural stress factor in this island environment (Mueller-Dombois and Lamoureux 1967, Vogl 1969). However, the very dense resprouting after clipping of herbaceous suckers is undoubtedly a new response. When goats are displaced after heavy browsing, koa saplings grow in dense thickets in which each individual becomes exposed to high intraspecific competition.

In contrast, the inability of woody saplings to resprout or form new leaders shows that koa is not really well adapted to browsing pressure. In a woody vegetation where browsing is a long-established factor, as for example in the monsoon forest-scrub vegetation of Ceylon, nearly all tree species were observed to respond to browsing by formation of new branches (Mueller-Dombois 1972b).

In 1968 a similar goat exclosure was constructed in the coastal lowland, in a summer-drought climate with 800 mm rain fall. Here the vegetation was dominated by the exotic, pantropical annual grass, Eragrostis tenella. Within two years the plant cover changed completely. Perennial bunchgrasses (Sporobolus africanus, Rhynchelytrum repens) became established. Among these was Heteropogon contortus, a grass introduced long ago by the Hawaiians. Also, woody chamaephytes began to grow here (Waltheria indica, Indigofera suffruticosa

and Cassia leschenaultiana). But most surprising was the appearance of a native legume vine, Canavalia kauensis, that was identified as a new endemic species (St. John 1972). In the third year Canavalia covered > 50% of the surface area in the exclosure (Mueller-Dombois and Spatz 1972). Currently, the exclosure vegetation is still in the chamaephyte-vine stage, and its future development is difficult to predict.

The remarkable fact is that a native species, never seen before in this area, could produce the dominant plant cover in spite of so many years of intensive goat grazing. Our current explanation is that the vine must have germinated and flourished in the general area from time-to-time in wet years which occur every 5-10 years. Periodic goat hunting, as practiced by the Park Service as control, may have aided in the survival of the vine. It is probable that several other native species have become extinct in the lowland grass area because their seed supply became exhausted from more or less continuous feeding of goats on shoots and seedlings.

However, both examples show that native plant recovery is at least in part still possible, when the introduced stress factor is removed. The Park Service is now fencing large areas in the lowland in an effort to recreate at least a partially native Hawaiian ecosystem.

CONCLUSIONS

Island ecology differs from continental ecology in several ways at the level of species interactions. Spatial distributions are often peculiar because only a few well-adapted species may exist in certain life form groups. Then their range or amplitude can be unusually broad because of an absence of competitors. Certain general niches, for example that of the phytophagous insects, are well filled and diverse. In those niches, there is greater

stability in the sense that penetration by exotics is much more limited. In poorly occupied niches, such as for example that of the soil arthropods or the grasses in disturbed rain forest habitats, sweeping invasion by exotics may occur. Even ecologically ill-adapted exotics may in such cases retain dominance, for example, the temperate Andropogon virginicus in disturbed rain forest habitats. However, in most cases so far observed among plants, exotic species do not penetrate easily into established native communities, unless new niches are created by direct disturbances, for example by cattle grazing in forests, digging in grassland, or by goat grazing and gradual elimination of certain species from the area. In these cases exotics may take over that are better adapted to such stresses, for example the annual Eragrostis tenella in the overgrazed lowland. On the other hand, removal of these man-introduced stresses still offers chances of part-recovery of native vegetation and associated biota.

Contrary to common opinion, many endemic island species are strong competitors. They would not be displaced or eliminated from their niche in the island ecosystems, if it were not for the new stress factors introduced by man. The island species evolved with such long standing stress factors as are associated with volcanism, fire in seasonally dry habitats and occasional hurricanes. The effects of volcanism resulted in superior adaptation of many native species to extreme edaphic conditions existing on volcanic rockland, where soil water regimes fluctuate almost instantly in direct relation to rainfall.

For preserving the uniqueness of island biota as much as it is left today, it is necessary only to eliminate the recently man-introduced stress factors that were not part of the spectrum of evolutionary stress factors of the isolated, oceanic island ecosystems before the arrival of technological

man.

The effect of evolution that is so clearly apparent in many ecological phenomena in island ecosystems is, of course, important also in continental ecosystems. However, ecological studies are concerned usually with processes and relationships that do not need a historical or evolutionary explanation. Thus, ecology and evolution are traditionally quite separate areas of research inquiry. In any fundamental study of island ecology, however, the evolutionary background cannot be ignored.

Moreover, future contributions to ecosystem theory will have to come not only from ecosystem process studies at the gross-structural level. At this level the answer will merely substantiate Tansley's (1920, 1935) concept of an ecosystem as a quasi-organism. Contributions to an understanding of ecosystems will also hardly be expected from studies of species populations out of context of their general niche. Such studies will describe ecosystems merely as a collection of parts. However, studies of species interactions within the context of their general niches and these within the context of the ecosystem as a whole, will provide answers to the degree and preciseness of web-like ramifications which are expected to make a community and its habitat an interacting system that consists of more than a collection of its parts.

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